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The dimensionality of stability depends on disturbance type

Running title: dimensionality of ecological stability

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52 ABSTRACT

53 Ecosystems respond in various ways to disturbances. Quantifying ecological stability therefore
54 requires inspecting multiple stability properties, such as resistance, recovery, persistence, and
55 invariability. Correlations among these properties can reduce the dimensionality of stability,
56 simplifying the study of environmental effects on ecosystems. A key question is how the kind of
57 disturbance affects these correlations. We here investigated the effect of three disturbance types
58 (random, species-specific, local) applied at four intensity levels, on the dimensionality of
59 stability at the population and community level. We used previously parameterized models that
60 represent five natural communities, varying in species richness and the number of trophic levels.
61 We found that disturbance type but not intensity affected the dimensionality of stability and only
62 at the population level. The dimensionality of stability also varied greatly among species and
63 communities. Therefore, studying stability cannot be simplified to using a single metric and
64 multi-dimensional assessments are still to be recommended.

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67 **Keywords:** Community model, persistence, resistance, invariability, recovery, extinction,
68 disturbance intensity, disturbance type, individual-based model

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GLOSSARY

State variables are variables used to quantify stability properties of a system, i.e. a population or a community in the context of this study. Examples of state variables are abundance (population level) and species richness or total abundance (community level).

Resistance is the degree to which a state variable is changed following a disturbance (Pimm 1984), here measured as the difference between a perturbed and a control system at the first sampling after the treatment (Hillebrand *et al.* 2018).

Recovery is the capacity of a system to return to its undisturbed state following a disturbance (Ingrisch & Bahn 2018), here measured as the degree of change in a state variable of a perturbed compared to a control system at the last sampling (Hillebrand *et al.* 2018).

Persistence is the existence of a system through time as an identifiable unit (Pimm 1984; Grimm & Wissel 1997), measured by the time during which a system maintains the same state (i.e., state variables within certain ranges) before it changes in some defined way (Donohue *et al.* 2016).

Invariability reflects the temporal constancy of a state variable following the disturbance, usually measured as the inverse of temporal variability of a state variable (Wang *et al.* 2017). Higher invariability indicates higher stability (Donohue *et al.* 2013).

Disturbance is a change in the biotic or abiotic environment that alters the structure and dynamics of a system (Donohue *et al.* 2016).

Stability is a multidimensional concept that tries to capture the different aspects of the dynamics of the system and its response to perturbations (Donohue *et al.* 2016). Here, we consider the following stability properties: resistance, recovery, persistence, and variability.

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91 The **dimensionality of stability** (DS) depends on the strength of correlations among
92 stability properties. Low correlation corresponds to high dimensionality. If dimensionality is
93 high, a single stability measure cannot be used as a sole indicator of the overall system stability
94 (Donohue *et al.* 2013).

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95 INTRODUCTION

96 Understanding the response of populations, communities, and ecosystems to fast, human-induced
 97 environmental changes is a key challenge (Carpenter *et al.* 2011; Higgins & Scheiter 2012;
 98 Scheffer *et al.* 2015; DeLaender *et al.* 2016). However, quantifying the stability of natural
 99 systems is challenging because stability is a multidimensional concept and requires measuring
 100 several stability properties such as *resistance*, *recovery*, *persistence*, and *invariability* (see
 101 Glossary, Pimm 1984; Grimm & Wissel 1997; Donohue *et al.* 2016). Correlation among these
 102 properties manifests the dimensionality of stability (DS): if the stability properties strongly
 103 correlate, the dimensionality is low, and *vice versa* (Donohue *et al.* 2013; Hillebrand *et al.* 2018,
 104 Fig. 1a,b). Theory underpinning DS is still in its infancy (Donohue *et al.* 2013) and relevant
 105 empirical evidence is only beginning to accumulate (Donohue *et al.* 2013; Hillebrand *et al.*
 106 2018). A key question is whether DS depends on the kind of underlying disturbance. Donohue *et*
 107 *al.* (2013) showed that when disturbed by consumer removal, DS increased in marine shore
 108 communities. At present it is unclear if such conclusions can be extrapolated to other kinds of
 109 disturbance.

110 There are many kinds of disturbance. Disturbance properties include: duration, spatial
 111 extent, intensity, frequency, and type (Turner 2010). According to their *duration*, two extreme
 112 classes of disturbance can be distinguished: pulse disturbances (e.g. fire or flooding) occur over a
 113 short time scale, relative to the typical speed at which a system changes, and press disturbances
 114 (e.g. global warming or exploitation) represent a constant, long-term change. Disturbance
 115 *intensity* reflects how much individuals / biomass are affected by an event over a period of time
 116 (Turner 2010). Disturbance *frequency* reflects how often disturbance events occur within a given

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Commenté [FDL1]: There's a space missing: 'De Laender', not 'DeLaender'

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117 time period. Examples of disturbance *types* are local vs. global, and selective vs. non-selective
118 disturbances (De Laender *et al.* 2016).

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119 Despite increasing understanding of how disturbances affect each single stability
120 property, we know little of how the kind of disturbance affects the relationships among multiple
121 stability properties, i.e. the dimensionality of stability (Donohue *et al.* 2013). Yet, such
122 knowledge is crucial for guiding efforts to monitor and manage natural systems. Indeed, if
123 several stability properties correlate strongly irrespective of the properties of disturbances acting
124 on them, the stability of the overall system reduces to one dimension (i.e. low DS, Fig. 1a). This
125 means that monitoring schemes could be optimized by quantifying only a few stability
126 properties. ~~Vice-versa~~Alternatively, if a system's stability properties are poorly correlated (i.e.
127 high dimensionality), inferring the system's overall stability requires measuring all ~~of~~
128 ~~them~~properties (Fig. 1b). Therefore, management of natural systems would profit from knowing
129 how DS is influenced by different disturbance properties. For example, an increase of
130 dimensionality with disturbance intensity would undermine the main assumption for detecting
131 tipping points (Dakos *et al.* 2012; Dai *et al.* 2015) through early warning signals (e.g. coefficient
132 of variation, temporal autocorrelation), which usually manifest the variability of a system.

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133 DS can be decomposed into pair-wise correlations among underlying stability properties
134 (Donohue *et al.* 2013; Hillebrand *et al.* 2018; Pennekamp *et al.* 2018). We generally expect
135 positive pair-wise correlations between invariability, resistance, recovery and persistence. For
136 example, ~~at the population level~~invariability and persistence are expected to correlate positively
137 ~~at the population level~~, because the higher the temporal constancy in population size, the more
138 likely the population is to persist (Ginzburg *et al.* 1982; Inchausti & Halley 2003). Similarly, at
139 the community level, the higher the temporal constancy in community composition, the more

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likely this community is to persist in its unchanged state. For arguments of why we expect other stability properties to correlate positively, see Table S1 in Supporting Information. Because pair-wise correlations are ‘constituents’ of DS, they are expected to depend on the same factors as DS: disturbance properties and the level of organization. Indeed, the sign of a pair-wise correlation between stability properties was shown to change when, instead of a single disturbance, two disturbance types were applied simultaneously to yeast populations (Dai *et al.* 2015). Also, pair-wise correlations measured at the community and ecosystem level differed in plankton communities disturbed by reduced light availability (Hillebrand *et al.* 2018). Understanding whether pair-wise correlations are affected similarly ~~by across disturbances~~ ~~irrespective of different~~ disturbance types and study systems would facilitate more efficient monitoring of the stability of natural systems.

Here, we used process-based, spatially-explicit models to assess how the intensity and the type of disturbance affect DS at the population and community levels. Our models are well tested and structurally realistic, and represent five different communities: a species-rich temperate grassland community, a temperate forest, an algae community, a boreal predator-prey system, and a host-pathogen system. The modelled communities varied in species richness (2 up to 86 species) and number of trophic levels (one or two). At both levels of organization we measured four stability properties: resistance, recovery, persistence, and invariability (Glossary, Fig. 2a-c, Table S2). We applied three disturbance types at four intensities. We distinguished disturbances that i) affect individuals selectively depending on their species identity, ii) affect individuals selectively depending on their location, and iii) affect all individuals similarly, irrespective of species identity or location (Fig. 2d,e,f). We tested the following hypotheses:

H1: At each level of organization, DS depends on disturbance type and intensity.

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H2: All investigated stability properties exhibit positive pairwise correlations (Table S1).

H3: At each level of organization, the pair-wise correlations depend on disturbance type and intensity.

166 **METHODS**

167 **Study systems**

168 We used models representing the dynamics of the following communities: temperate
169 forests (Bohn *et al.* 2014), a marine algal community (Baert *et al.* 2016a), a species-rich
170 temperate grassland (May *et al.* 2009), a boreal predator-prey system of mustelids and voles
171 (Radchuk *et al.* 2016a), and a temperate host-pathogen system of classical swine fever (CSF)
172 virus affecting wild boar populations (Kramer-Schadt *et al.* 2009; Lange *et al.* 2012). All of these
173 models had previously been parameterized to mimic the conditions of the respective natural
174 communities (Table S3). All models have three aspects in common: 1) they are spatially explicit,
175 describing the location of habitat patches and movement of individuals among them; 2) they
176 include demographic stochasticity; and 3) the smallest modelled entity is the individual (except
177 for the model simulating an algae community, which is based on Lotka-Volterra equations with a
178 dispersal component; Supplementary Text T1). In addition to demographic stochasticity, two
179 models (a host-pathogen model and a model of temperate forests) also include environmental
180 stochasticity. Temperate grassland was modelled in two ways: using the original IBC-grass
181 model (May *et al.* 2009) and a modified version that incorporates intra-specific trait variation
182 (from now on referred to as Grassland ITV, Crawford *et al.* 2018). We thus used six models that
183 represented five study systems. An advantage of using models that have been previously
184 developed is ~~because that~~ those models have already been tested and verified for ~~respective~~
185 natural systems. We provide short summaries of the main processes included in each model in
186 ~~the~~ Supplementary Methods, and more detailed descriptions of the models in the Supplementary
187 Texts T1-T5.

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189 Disturbances

190 The previously published versions of the models, parameterized to reflect a stochastic
191 quasi-equilibrium state (Nolting & Abbott 2016), were used as a control (no disturbance). We
192 implemented disturbance as a one-time (pulse) removal of individuals. We implemented three
193 types of disturbance (Fig. 2d, e, f): *random disturbance* affected individuals randomly,
194 irrespective of their species identity and location. This disturbance type reflects a non-selective
195 disturbance (De Laender *et al.* 2016). The *rare species removal disturbance* reflects the
196 assumption that the rarest species are most extinction-prone (Solan *et al.* 2004) and is applied to
197 species inversely to their population abundance ranks. This disturbance type was not possible in
198 the wild boar - virus model (Supplementary Methods). The *spatially-structured disturbance*
199 mimicked a localized disturbance by randomly selecting a point for the centre of the disturbance
200 and then gradually increasing the disturbance radius around this point until the disturbance
201 affected the target number of individuals (as defined by the disturbance intensity). We have
202 implemented disturbance types via removal of individuals because this is a generic process that
203 is inherent to several real-world disturbances, such as habitat fragmentation, hunting, culling and
204 pollution. Using removal of individuals allows for comparability of results among the models as
205 they differ in their processes. Therefore, removal of individuals was the best compromise among
206 the relevance of the disturbance type and comparability of results among the systems.

207 Each disturbance type was implemented at four intensities, reflecting increasing
208 proportions of the community that were removed (0.1, 0.2, 0.3 and 0.4 respectively). An upper
209 bound of intensity was chosen via preliminary tests scanning a larger range of intensities, which

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showed that at a disturbance intensity > 0.5 , all species in our 2-species systems went extinct, complicating the measurements of all stability properties.

We ensured the comparability of the results in terms of the temporal scales among our study systems by scaling the duration of the simulation runs to the average generation length of all the species in the community (Pimm 1984). We used 30 average generations of the control as a ‘burn-in’ phase, after which either the control or one of the disturbance type scenarios were run for the next 60 generations, which was enough for majority of the species to attain either previous or a new stochastic quasi-equilibrium state (based on Gelman-Rubin diagnostics, Supplementary Figs. S1-S3, Supplementary Methods). The disturbance was applied in the first time step immediately after the ‘burn-in’ phase. We ran 30 replicates of each of the 13 scenarios (the control plus three disturbance types crossed with four levels of disturbance intensity) to account for the stochasticity inherent in the models. These 30 replicates were sufficient to capture effects that are due to disturbances and not merely a result of stochasticity (Supplementary Methods and Figs. S4-S7). The ‘burn-in’ phase was discarded when calculating the stability properties.

Stability properties

At both the community and population level, we quantified four stability properties: *resistance*, *recovery*, *persistence* and *invariability* (Glossary, Fig. 2a-c, Table S2). We quantified stability properties analogously at both levels of organization. At the community level as state variable we used community composition, and at the population level we used abundance. We here detail how stability properties were measured at the community level, for details on how it was done at the population level please refer to Supplementary Methods.

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232 *Resistance* was measured as Bray-Curtis similarity of the community composition
 233 between treatment and control at the first sampling after treatment (time step 1, Hillebrand *et al.*
 234 2018). *Resistance* ranges between 0 and 1 with 1 reflecting maximum resistance (100%
 235 similarity between treatment and control). *Recovery* reflects the degree of restoration of the
 236 system at the end of the time series and was measured as Bray-Curtis similarity of the
 237 community composition between treatment and control at the final sampling (time step 60,
 238 Hillebrand *et al.* 2018). Analogously to resistance, recovery ranges between 0 and 1, with 1
 239 reflecting a full recovery. *Persistence* was measured as the time during which the community
 240 composition in a treatment remains within 90% of the Bray-Curtis similarity with the
 241 composition of the control community. We scaled the original persistence values (min = 1, max
 242 = 60) by dividing them by their theoretically possible maximum (60), so that persistence ranges
 243 from 0 (the similarity between the treatment and control is < 0.9 in the first time step) to 1
 244 (maximum persistence, a system remains within 90% of similarity during the whole period).
 245 Temporal *invariability* (Wang *et al.* 2017) was measured as the inverse of standard deviation of
 246 residuals from the linear model regressing the Bray-Curtis similarity between the treatment and
 247 control communities on time (Hillebrand *et al.* 2018). When temporal invariability is higher, i.e.
 248 when community composition fluctuates less around the average trend, the stability is higher. In
 249 Supplementary Methods we explain the choice of 1) Bray-Curtis similarity as a particularly
 250 suitable state variable for measuring stability at the community level (Donohue *et al.* 2013;
 251 Hillebrand *et al.* 2018) and 2) the threshold of 90% of Bray-Curtis similarity to measure
 252 persistence.

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Dimensionality of stability

We quantified DS using multidimensional ellipsoids based on the covariance matrices among all stability properties (Donohue *et al.* 2013). The covariance matrices were constructed using the 30 replicates per scenario (at the community level) and per species nested within each scenario (at the population level). Since disturbances may affect both the volume and the shape of such ellipsoids (Donohue *et al.* 2013, Fig. 1a-c), we considered both. We used semi-axis lengths to characterize the shape of ellipsoids. The semi-axis length a_i was measured as $a_i = \lambda_i^{0.5}$, where λ_i is the i^{th} eigenvalue of the covariance matrix for a given scenario (i.e. a combination of the disturbance type and intensity) at the community level and for each species within each scenario at the population level. Ellipsoid volume was calculated as $V = \frac{\pi^{n/2}}{\Gamma(\frac{n}{2}+1)} \prod_{i=1}^n (\lambda_i^{0.5})$, where n is the dimensionality of the covariance matrix. Prior to the calculation of the ellipsoid volume, each set of semi-axis lengths was standardized by dividing all of them by the maximum length within a set, so that the maximum standardized length equalled 1. This allowed us to calculate the largest volume that was theoretically possible (i.e. all of the standardized semi-axis lengths are 1), which reflects a perfect spheroidal shape and, therefore, high DS. By dividing the actual ellipsoid volume by the theoretical maximum, we obtained a proportional volume. This proportional volume varies between 0 (a ‘cigar’-like shape of ellipsoids, Fig. 1a), and 1 (a perfect sphere, Fig. 1b), reflecting low and high DS, respectively. Characterization of multidimensional ellipsoids based on covariance matrices relies on the assumption of linear relationships among stability properties (Supplementary Methods). In our case this assumption is satisfied for most study systems and disturbance types (e.g. Figs. S8-S15).

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To test the effect of disturbance properties on DS (H1) we fitted generalized mixed-effects models (Gamma distribution) with either ellipsoid volume or semi-axis length (per each rank, Fig. 1c) as a response (Supplementary Methods). As fixed effect predictors we included disturbance type (as a factor) and intensity (as a continuous variable). At the community level, we included study system as a random slope and at the population level, the random slope structure consisted of the species nested within the study system. We tested for the significance of fixed-effect terms using likelihood-ratio tests (LRT), but in our interpretations focused on effect sizes, because our study is based on simulations and virtually anything can become significant given enough replicates. At the community level, there was no variation in persistence for at least one disturbance type in the three study systems (persistence was 0 in all replicates of a rare species removal disturbance in both grassland systems and it was 1 in all replicates of random disturbance and rare species removal of the algae system). This precluded calculation of semi-axis lengths and ellipsoid volumes using all four stability properties (i.e. four dimensions) for these study systems. Therefore, we first fitted models using all four dimensions with only three study systems (forest, vole-mustelid, and wild boar-virus), and then used three dimensions (excluding persistence) to fit models with all six study systems. The results from both analyses are qualitatively the same. The results based on three dimensions are presented in the main text, and those based on four dimensions in Fig. S16, Tables S4 and S5.

Pair-wise correlations

To test whether all pair-wise correlations among stability properties were positive (H2) and affected by the disturbance properties (H3), we calculated Spearman-rank correlation for each pair of stability properties obtained for each of the 13 scenarios at the community level. Similarly, at the population level, Spearman-rank correlation was calculated for each species

298 within each scenario. Next, we transformed these Spearman-rank correlations into Fisher's z
299 scores to improve their normality and to avoid any disproportionate influence of extreme values,
300 and used them as effect sizes in the meta-analysis (Koricheva *et al.* 2013). We fitted mixed-
301 effects meta-analytic models (Gaussian distribution) with the fixed effects of disturbance type (a
302 factor), disturbance intensity (a continuous variable), and an interaction between them. At the
303 community level, the models included the study system and replicate as random intercepts. At
304 the population level, also species identity was included as a random intercept. All meta-analytic
305 mixed-effects models were fitted with the library *metafor* in R (Viechtbauer 2010). All analyses
306 were conducted in R 3.4.2 (R 2017).

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RESULTS

Effect of disturbance properties on the dimensionality of stability

At the community level, neither disturbance type nor intensity affected DS (as measured by semi-axis lengths, Fig. 3a & Fig. S17a; and ellipsoid volumes, Fig. 4a & Fig. S18a; Table S4). However, study systems varied in their DS, as measured by semi-axis lengths (Table S6, Fig. 3a) or ellipsoid volumes (Fig. 4a). While grassland and forest communities were characterized by high DS (Fig. 4a), corresponding to spheroid-looking stability ellipsoids (Fig. S19a,b), vole-mustelid and algae communities had low DS, corresponding to a ‘cigar’-like ellipsoids.

At the population level, the disturbance intensity did not affect DS (Fig. S18b), while disturbance type did (Table S4). Random disturbance increased DS (Fig. 4b). This was also reflected in the differences among semi-axis lengths: under random disturbance, the semi-axis lengths of the 1st rank were shorter ~~compared to~~ than for other disturbance types, and the semi-axis lengths of the 3rd and 4th order were longer ~~than for~~ compared to other disturbance types (Fig. 3b). At the population level, DS varied among study systems and species (Fig. 4b, Table S5).

Pair-wise correlations between stability properties

At the community level, pair-wise correlations were on average positive (supporting H2) and three out of six correlations were affected by disturbance properties (supporting H3, Fig. 5a). ~~The Correlation correlation~~ of recovery with resistance and ~~of~~ recovery with invariability depended on the disturbance type, with positive correlations under random disturbance and very weak correlations (around 0) under spatially-structured disturbance. ~~The Correlation correlations~~

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between invariability and persistence became weaker and approached 0 as disturbance intensity increased.

At the population level, two pair-wise correlations were on average negative, three were positive, and one correlation was close to 0 (Fig. 5b-d). All pair-wise correlations were affected to a certain degree by disturbance type (Table S7). Additionally, disturbance intensity interacted with disturbance type in its effect on one correlation (invariability with recovery, Fig. 5c) and affected another one (invariability with resistance) in an additive way (Fig. 5d). There was no coherent pattern in how disturbance type modulated different pair-wise correlations.

DISCUSSION

We tested whether the correlation structure among stability properties was affected by the disturbance properties across five communities, differing in species richness and number of trophic levels. ~~Contrary to our expectation (H1), At the community level,~~ we did not find an effect of ~~the~~ disturbance properties on the dimensionality of stability- ~~(DS) at the community level(DS, H1)~~. At the population level, DS was higher under random disturbances. Additionally, at both levels of organization DS varied largely among study systems. At the community level, as expected (H2), we found generally positive correlations among different stability properties. In contrast, at the population level, the sign and magnitude of correlations were highly heterogeneous. Finally, pair-wise correlations at both levels depended on the disturbance properties, mainly on disturbance type, supporting our hypothesis (H3), although the effect sizes were smaller at the community level.

Dimensionality of stability at the community and population level

We did not find any effect of disturbance properties on DS at the community level. However, our findings reveal high heterogeneity in DS among study systems. For 4 of the 6 study systems, community stability was a highly-dimensional concept (Fig. 4a), suggesting that monitoring these systems requires measuring multiple stability properties. A promising avenue for future research would be investigating whether – and what – properties of a system predict its DS. At the community level, our findings indicate that such candidates of system properties as species richness and number of trophic levels do not discriminate the systems with low and high DS (Fig. S20a,b). Indeed, our two species-poor systems (‘vole-mustelid’ and ‘wild boar-virus’) exhibited strikingly different DS (Fig. 4a). Similarly, we observed both high and low DS in communities with either one (e.g. ‘algae’ vs ‘grassland’) or two trophic levels (‘vole-mustelid’

360 vs ‘wild boar-virus’). Taken together our results indicate that, although DS does not depend on
361 disturbance properties, measuring multiple stability properties is necessary until we can establish
362 whether and what system properties underlie DS.

363 Similarly to the community level, DS was highly context-dependent at the population
364 level: in addition to variation among disturbance types, we also found high heterogeneity among
365 study systems and species (Table S5), with the highest dimensionality under random disturbance.
366 Although this type of disturbance may seem of little relevance to real-world applications, it is
367 closely mimicked by the application of certain chemicals (Roessink *et al.* 2006; DeLaender *et al.*
368 2016), and therefore its effects on DS deserve further investigations. Interestingly, our findings
369 indicate that species-poor systems may generally have higher DS (Fig. S20d). Since population
370 invariability is known to be lower in species-rich systems (Gonzalez & Descamps-Julien 2004;
371 Jiang & Pu 2009; Gross *et al.* 2014), it is likely that species richness modulates the relations of
372 population-level invariability with other stability properties. However, as we did not
373 experimentally manipulate species richness in this study, this is a hypothesis to be tested by
374 future research.

375 Reflecting the context-dependence of DS, all pair-wise correlations between population
376 stability properties depended on the disturbance type, and additionally two out of six depended
377 on the disturbance intensity (Fig. 5b-d). These results corroborate earlier analytical derivations
378 (Harrison 1979) that showed that the relation between population resilience and resistance
379 depends both on density-dependence and on the environmental sensitivity of the population
380 growth rate. In fact, the high heterogeneity found in the meta-analytic models testing the context-
381 dependence of the pair-wise correlations between population stability properties (Table S8)
382 points towards species-specific differences which may be due to differences in density

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dependence (as found by Harrison 1979) or any other species-specific properties (e.g. population growth, carrying capacity).

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From a monitoring perspective, the context-dependence of the correlative structure among stability properties at the population level (H3) means that quantification of population stability as a whole requires measurements of multiple stability properties unless the context-dependence of these properties was established beforehand. Even though this may sound like a daunting task, it is already a well-established practice within population viability analysis (Beissinger & Westphal 1998; Pe'er *et al.* 2013). In such studies, multiple stability properties such as time to extinction, minimum viable population size, mean population size, etc. are jointly reported as a rule (Pe'er *et al.* 2013).

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Across-system differences in dimensionality of stability and plausible mechanisms

We did not find any effect of disturbance type on DS at the community level but higher DS was observed for random disturbances at the population level. Although these general results hold across the five different study systems, the largest heterogeneity in DS was revealed among study systems. As mentioned above, this heterogeneity cannot be explained by system properties as species richness and number of trophic levels. Two general mechanisms behind the responses of ~~system's~~ DS to disturbance can be distinguished: changes in the intensity of species interactions and changes in the degree of stochastic dynamics of the system. Although we have not experimentally manipulated these mechanisms here, we discuss the revealed differences in DS among systems in light of these mechanisms.

404 Changes in the intensity of species interactions could explain the link between
 405 disturbances and DS. Indeed, previous research demonstrated that inter- and intra-specific
 406 interactions affect community stability (McCann 2000; Thébault & Loreau 2005; Barabás *et al.*
 407 2016). Moreover, the effect of changes in species interactions on DS may differ depending on
 408 the primary type of interactions within a system (competitive vs. trophic), because vertical
 409 diversity was shown to modulate the biodiversity – stability relationship (Reiss *et al.* 2009;
 410 Radchuk *et al.* 2016b)+Wang and Brose’s Ecology Letters from last year (‘vertical diversity
 411 hypothesis’). Indeed, in our simulations, the removal of a rare species ~~removal in from~~
 412 communities driven by competitive interactions (algae, grassland and forest systems) resulted in
 413 lower DS (Table S9) both at the community and population level. The mechanism underlying the
 414 lower DS in these communities after removal of rare species (Table S9) may be an increasing
 415 strength of competitive interactions among the remaining species.

416 Stronger competitive interactions presumably occurring after removal of rare species,
 417 may in turn lead to more deterministic dynamics of the system. The degree of dynamic system
 418 behaviour may itself affect DS. Indeed, ~~a~~ more stochastic population dynamics likely results in
 419 weaker pair-wise correlation among stability properties, thus leading to higher DS. In support of
 420 this expectation, we found increased DS after a spatially-structured disturbance in systems
 421 consisting of two strongly interacting species at different trophic levels (Table S9). Such two-
 422 species communities are presumably more prone to stochastic effects than multispecies
 423 communities, and therefore exhibit the above-described behaviour. To closer inspect the relation
 424 between system stochastic behaviour and DS, we used population abundance and community
 425 evenness the following as proxies of the influence of demographic stochasticity ~~at the on~~
 426 populations and community communities level, respectively: ~~population abundance and~~

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427 ~~community evenness~~ (Supplementary Methods). Overall, we found an increase in DS under
428 higher stochasticity at both population and community levels (Fig. S21-S22). However, the
429 responses varied among disturbance types, study systems and species (for the population-level
430 DS; Figs S23-S24). ~~Importantly, these findings have to be treated with caution because~~ Clearly,
431 we did not experimentally vary stochasticity, as this was not the goal of our study. ~~and Future~~
432 future research in this direction is warranted.

433 The change of system behaviour from stochastic to deterministic and vice versa may also
434 be caused by dispersal. Dispersal plays an important role in stochastic community assembly
435 (Chase 2007) and has recently attracted attention in the context of metapopulation and
436 metacommunity stability (Dai *et al.* 2013; De Raedt *et al.* 2017; Gilarranz *et al.* 2017; Zelnik *et*
437 *al.* 2018). Further, functional diversity, in particular response diversity and correlations among
438 effect and response traits were suggested as mechanisms potentially explaining pair-wise
439 correlations between stability properties (Pennekamp *et al.* 2018). Additionally, some of the
440 observed differences in system responses may be due to the model type used and not especially
441 because of the system-specific characteristics. Thus, models such as the Lotka-Volterra model
442 (used for the algae community) result in more deterministic community dynamics compared to
443 individual-based models that incorporate more stochasticity at different levels and processes.
444 Indeed, the algae model showed a strikingly clear response as compared to other systems (Table
445 S9, Fig. 4a), which may be explained by deterministic system behavior.

446 Challenges and future research

447 Our study identified several challenges associated with measuring DS. ~~for example Amongst~~
448 those are: quantifying the relationships among stability properties that are non-linearly related;
449 choosing appropriate state variables to measure stability properties; choosing specific stability

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Commenté [FDL2]: Not clear what we mean here.

450 properties at each level of organization; deciding on the disturbance types and intensity levels. A
 451 wide variety of stability properties is used in the literature, and different approaches to
 452 quantifying them are available (Grimm & Wissel 1997; Ingrisch & Bahn 2018). For example, we
 453 have chosen to measure resistance at the first time step after disturbance. An alternative would be
 454 to measure resistance at the time step when the response is the strongest, which, naturally, will
 455 differ among species and systems. Comparison of how existing stability properties and methods
 456 to measure them perform under different conditions and unification of such approaches ~~must be~~
 457 an avenue for future research (Ingrisch & Bahn 2018). Further, we here focused on disturbance
 458 by removing individuals mainly for the sake of comparability of results among systems and
 459 models. What the implications of other disturbance types are, in particular the addition of
 460 individuals (stocking) and habitat fragmentation ~~are~~, and how they compare to the removal of
 461 individuals, remains to be tested.

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462 Further, a future research agenda on DS should include: a mechanistic (?) investigation of
 463 interactions among disturbance types, developing approaches to quantify non-linear responses of
 464 systems to disturbance, and non-linear trade-offs among dimensions of stability. Importantly,
 465 understanding the mechanistic mechanisms underpinnings ~~of~~ the responses of DS requires that
 466 future experiments on real and *in-silico* systems manipulate potential mechanisms, generally the
 467 strength and sign of species interactions, and the stochasticity of the system's dynamics (which
 468 may be achieved by manipulating response diversity, dispersal abilities and environmental
 469 sensitivities of the species in the community). [What I cut may be a bit too evident] Preferably,
 470 ~~such experiments would use a factorial design combining several tentative mechanisms of DS,~~
 471 ~~while measuring population or community dynamics at a fine temporal resolution.~~ For such
 472 experiments the use of modelling studies, as done here, seems ~~indispensable~~ a useful ay forward.

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473 because collection of such data empirically is feasible only in micro- and mesocosm settings
474 (Baert *et al.* 2016b; Garnier *et al.* 2017; Karakoç *et al.* 2018; Pennekamp *et al.* 2018).
475 Importantly, although measuring DS was rather easy in our modelling study, empirical studies
476 may be limited because of the difficulty to measure multiple stability properties in natural
477 systems.

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478 There is a large, continually growing literature on stochastic population, community and
479 metacommunity ecology, which considers relationships between (usually only two) different
480 stability properties at different levels of organisation, and includes age-, stage- and spatial
481 structure (e.g. Petchey *et al.* 1997; Ovaskainen & Hanski 2002; Inchausti & Halley 2003; de
482 Mazancourt *et al.* 2013; Arnoldi *et al.* 2016; Wang & Loreau 2016). We here point out avenues
483 for extending the current research and underline that both empirical and theoretical efforts are
484 needed.

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485 Conclusions

486 We used process-based models developed and parameterized to reflect a range of natural
487 systems to test the effect of disturbance properties on the dimensionality of stability measured at
488 the population and community level. Our findings indicate that in the majority of cases
489 monitoring of population and community stability will require quantification of multiple stability
490 properties, and the use of a single proxy is not justified (Donohue *et al.* 2013; Hillebrand *et al.*
491 2018). Moreover, we also show that the correlations among stability properties may differ
492 depending on the level of organization, which was demonstrated only once until now by
493 Hillebrand *et al.* (2018), ~~who considered~~ who compared the community ~~and-and~~ ecosystem
494 levels. We believe that our study will catalyze the emerging research on the relations among
495 stability properties measured at different organization levels, and temporal and spatial scales,

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496 which in turn will lead to the development of a comprehensive theory of community and
497 population dynamics further from their equilibrium.

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FIGURES

Figure 1. Schematic representation of the dimensionality of stability. (a,b) Hypothetical multidimensional ellipsoids reflecting systems with low (a, black) and high (b, brown) dimensionality, and their respective semi-axis lengths (c_x), reflecting the amount of variation along each axis. The axes are ranked from the one that explains most variation to the one with the least variation (Donohue et al. 2013).

Figure 2. (a-c) Four stability properties measured at the community (a) and population (b, c) level in this study. Red vertical dotted line highlights the time step at which the disturbance (= treatment) occurs (for demonstration purpose here generation 4). Resistance (Res) and recovery (Rec) at the community level are measured as $BC\left(\frac{Comp_t}{Comp_c}\right)$, where BC is Bray-Curtis similarity, and $Comp_x$ is community composition in either control ($x = c$) or treatment ($x = t$), measured at the time steps indicated by green (Res) and blue (Rec) vertical dashed lines, respectively. Resistance and recovery at the population level are measured as $\ln\left(\frac{Ab_t}{Ab_c}\right)$, where Ab_x is abundance in either control ($x = c$) or treatment ($x = t$), measured at the time steps indicated by green (Res) and blue (Rec) vertical dashed lines, respectively. The grey solid line depicts a fitted model that is used to assess invariability (Inv), for demonstration purpose only two residuals are highlighted. An orange arrow shows how (a) $T_{0.9}$ at the community level and (c) TTE (time to extinction) at the population level are obtained. Persistence at the population level is calculated as: $Perc_{pop} = \frac{TTE}{T_{max}}$; and at the community level: $Perc_{com} = \frac{T_{0.9}}{T_{max}}$, where T_{max} is the maximum duration (here 16 generations) (for more details see Methods and Table S2). (d-f). Disturbance types used in this study: random (d), rare species removal (e) and spatially-structured disturbance (f). Each disturbance type is shown at 20% disturbance intensity. A two-patch system is depicted with

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each symbol representing an individual and the shape reflecting the species identity. Empty symbols indicate the individuals that would be removed under each disturbance. A circle in (f) shows a radius of a spatially-structured disturbance type.

Figure 3. At the community level (a) disturbance type did not affect semi-axis lengths, whereas at the population level (b) semi-axis lengths were affected by the disturbance type. High DS was found under random disturbance, as indicated by the semi-axis lengths of the 1st rank on average shorter compared to other disturbance types, and the semi-axis lengths of the 3rd and 4th order longer compared to other disturbance types. We observed large variation among study systems in their semi-axis lengths. Results are shown for disturbance intensity = 0.2 (since there is no effect of intensity). The semi-axis lengths are shown for each rank separately (1-3 for the community and 1-4 for the population level). The dots show outliers. Study systems are described in Table S3, different colours reflect different disturbance types: spatially-structured, rare species removal and random disturbance.

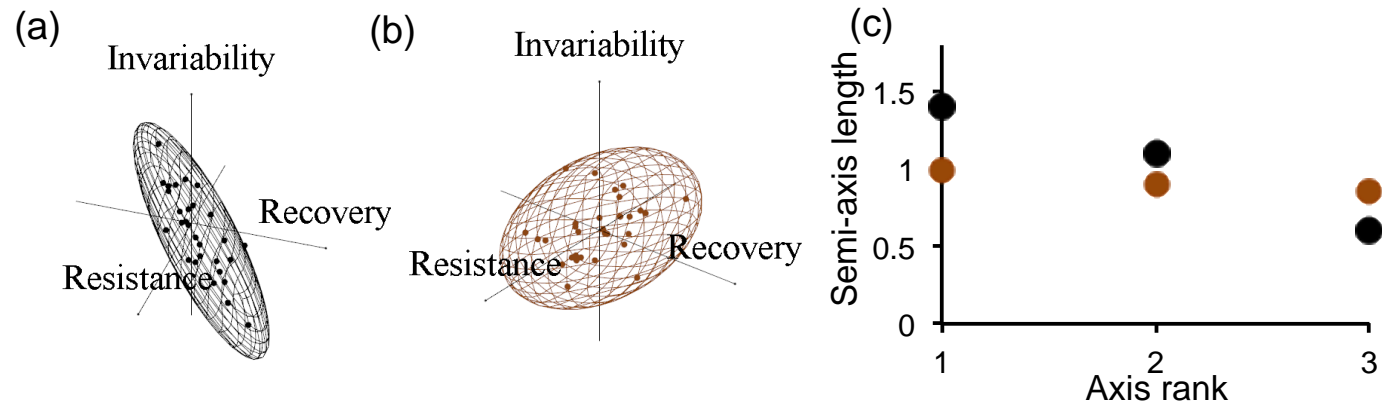
Figure 4. Disturbance type did not affect proportional ellipsoid volumes at the community (a), but did affect them at the population (b) level: random disturbance increased the dimensionality of stability, as visible from larger ellipsoid volume. We observed large variation among study systems in their ellipsoid volumes, especially at the community level. Results are shown for disturbance intensity = 0.2 (since there is no effect of intensity). At the maximum proportional volume (= 1) DS is highest, corresponding to a perfect sphere. The lower the proportional volume the lower is DS, with ellipsoid shape changing via a 'frisbee'-looking to a 'cigar'-like shape. Ellipsoids at the community and population level are calculated using three and four dimensions, respectively (see Methods). Abbreviations are as in Fig. 3.

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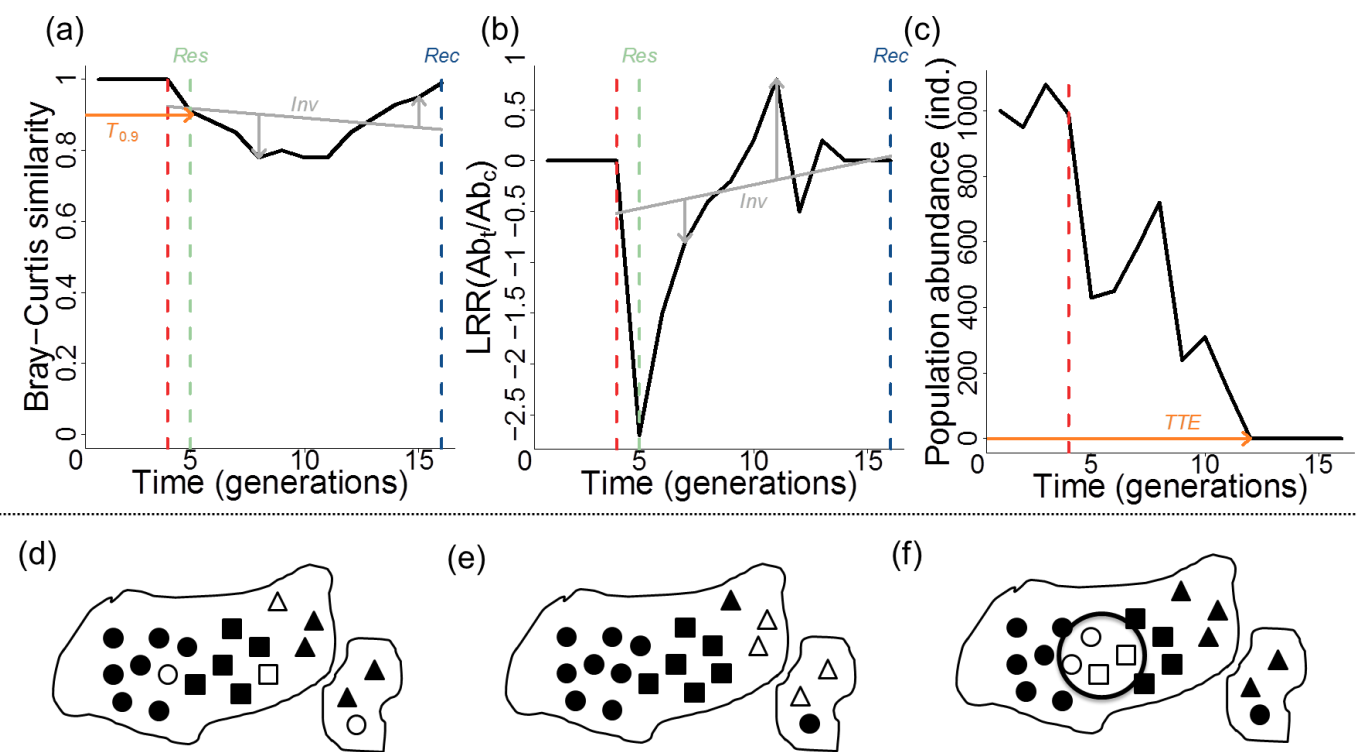
685 Figure 5. Effects of disturbance type and intensity on Fisher’s z scores representing all
686 pair-wise correlations between stability properties at the community (a) and population (b-d)
687 level. At the community level, majority of correlations were positive (a), whereas at the
688 population level, the sign and magnitude of correlations were highly heterogeneous (b-d).
689 Disturbance type affected two out of six correlations at the community level and all correlations
690 at the population levels. Shown are the effect sizes (and their 95 % CI) from the model that
691 described the data the best. For those correlations not affected by tested variables the effect size
692 obtained with the model including the intercept only is shown (i.e. the effect across all study
693 cases). Abbreviations are as in Fig. 3.

694

Figure 1.

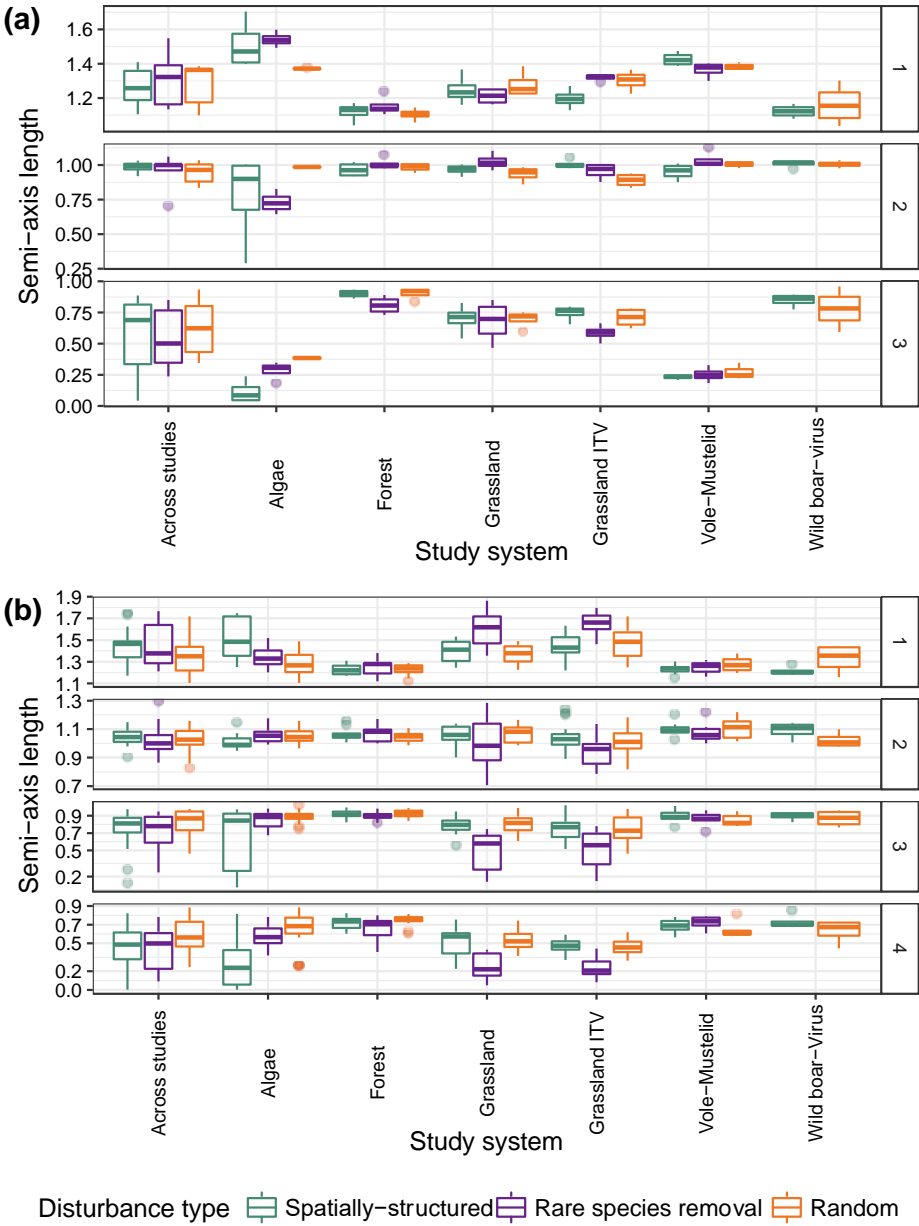


700 Figure 2.

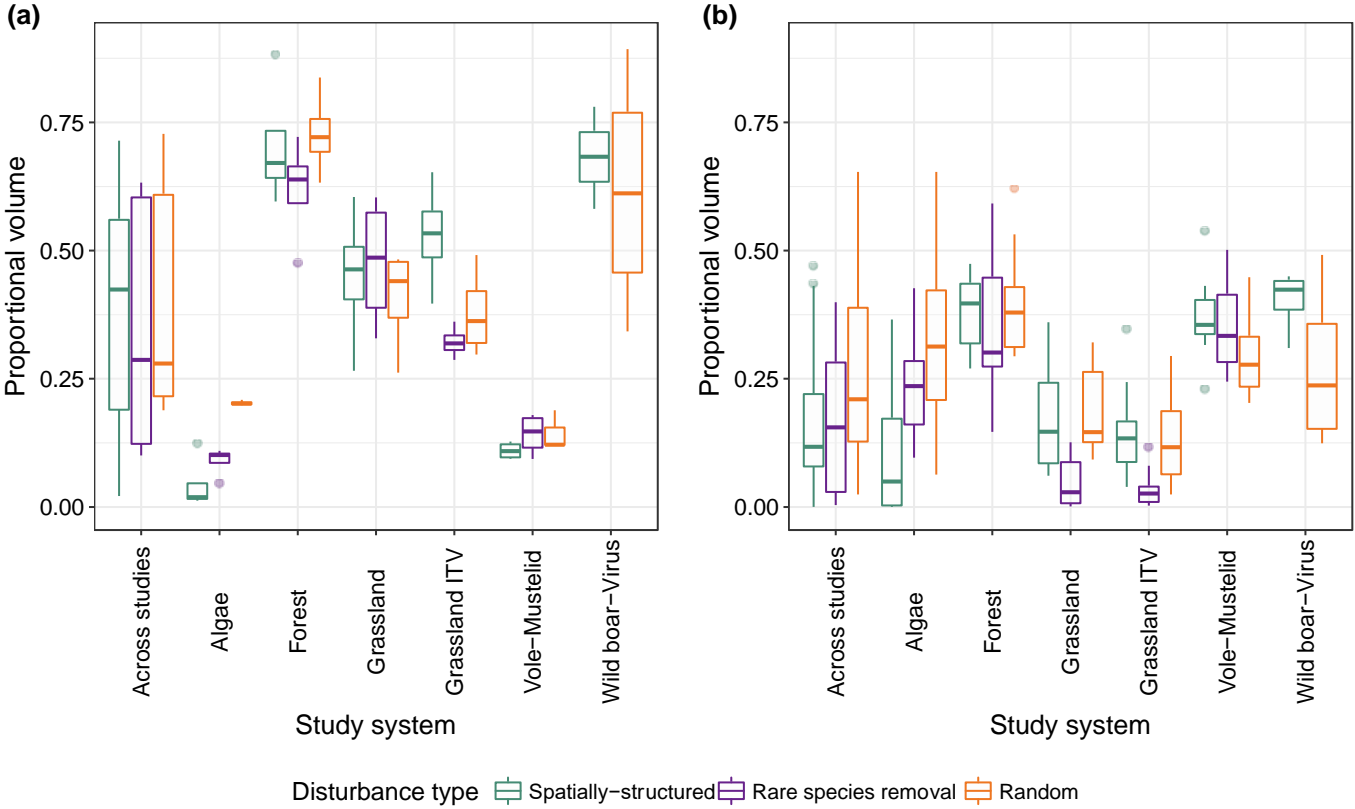


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703 Figure 3.



705 Figure 4.



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707 Figure 5.

